

A revision of *Vermivora* (Parulidae), with the description of a new genus

by George Sangster

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The genus *Vermivora* Swainson, 1827, currently comprises nine species (Curson *et al.* 1994, AOU 1998, Dickinson 2003). The genus includes three rather colourful species found in eastern North America—*V. pinus* (Linnaeus, 1766), *V. chrysoptera* (Linnaeus, 1766) and *V. bachmanii* (Audubon, 1833), of which the latter is possibly extinct—and six rather plain species whose ranges are concentrated on northern and western North America: *V. peregrina* (A. Wilson, 1811), *V. celata* (Say, 1823), *V. ruficapilla* (A. Wilson, 1811), *V. virginiae* (S. F. Baird, 1860), *V. crissalis* (Salvin and Godman, 1889) and *V. luciae* (J. G. Cooper, 1861). Two further species, *Parula gutturalis* (Cabanis, 1860) of Costa Rica and western Panama, and *P. superciliosa* (Hartlaub, 1844) of Central America, are currently placed in *Parula* Bonaparte, 1838 (Curson *et al.* 1994, AOU 1998, Dickinson 2003) but have been included in *Vermivora* by some authors (e.g. Hellmayr 1935, Lowery & Monroe 1968, Webster 1997).

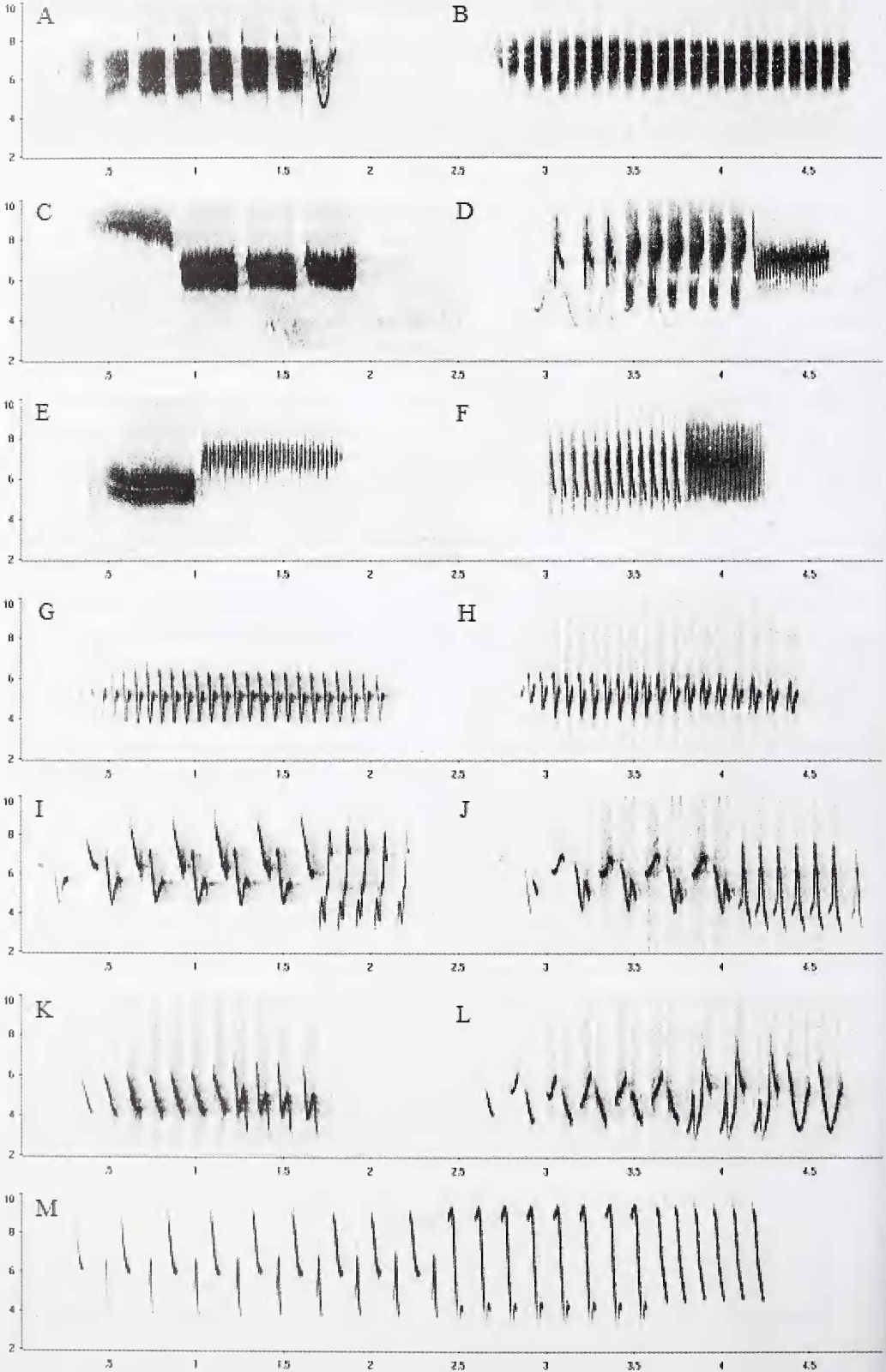
Systematics

Three independent molecular phylogenetic studies indicate that *Vermivora*, as presently constituted, is polyphyletic. Avise *et al.* (1980) used protein differentiation to construct a phylogeny of 28 species of parulids, including four species of *Vermivora*. They found sister-group relationships between *V. pinus* and *V. chrysoptera* and between *V. celata* and *V. peregrina*. However, these two pairs were not closely related. Klein *et al.* (2004) examined mitochondrial cytochrome-*b* sequence data (1,140 bp) of 50 parulids, including all extant species of *Vermivora* plus *P. gutturalis* and *P. superciliosa*. Their results corroborated and extended those of Avise *et al.* (1980): *V. pinus* and *V. chrysoptera* were found to be sister taxa, whilst the six 'plain' species of *Vermivora* formed a second, distantly related clade. Lovette & Hochachka (2006), who examined mitochondrial sequence data (4,116 bp) of 43 North American parulids, also found a sister-group relationship between *V. pinus* and *V. chrysoptera* and a distantly related clade of 'plain' species of *Vermivora*.

Recent studies have also clarified the position of *P. gutturalis* and *P. superciliosa*. Klein *et al.* (2004) found that *P. gutturalis* and *P. superciliosa* are sister to the clade of plain species of *Vermivora*, and are not closely related to either *P. americana* or *P. pitiayumi* with which they are currently included in the genus *Parula*. Another molecular study based on mitochondrial DNA sequences found that *P. gutturalis* clustered with *V. ruficapilla*, rather than with *P. americana* (Lovette & Bermingham 2002). The latter study included only three species of *Vermivora* and *Parula* but was based on long DNA sequences (3,638 bp). In a study of the skeletal characters of New World warblers, Webster (1997) concluded that *P. gutturalis* and *P. superciliosa* belong in *Vermivora* rather than *Parula* based on their long retroarticular processes.

Taxonomy

The polyphyly of *Vermivora* and the position of *P. gutturalis* and *P. superciliosa* close to the 'plain' clade of *Vermivora* warblers warrant a revision of the generic limits of *Vermivora*. The evidence summarised above indicates that the eastern clade (*V. pinus*, *V. chrysoptera*)



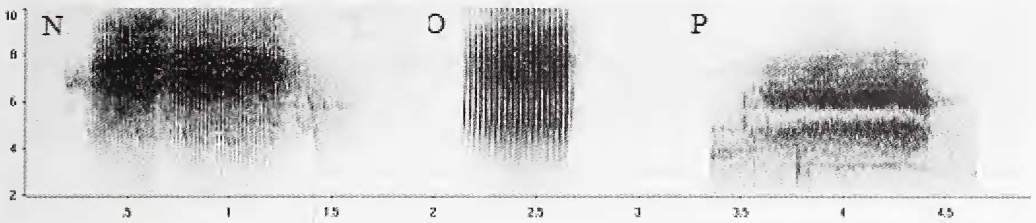


Figure 1. Sonograms of songs of *Vermivora* (A–F), *Leiothlypis* (G–M) and *Oreothlypis* (N–P) warblers. (A) *Vermivora bachmanii*, Virginia, USA, May, Arthur A. Allen (Borrer & Gunn 1985); (B) *V. bachmanii*, South Carolina, USA, May, Stuart Keith (Borrer & Gunn 1985); (C) *V. chrysoptera* type 1 song, Ohio, USA, May, Donald J. Borrer (Borrer & Gunn 1985); (D) *V. chrysoptera* type 2 song, New York, USA, May, Lang Elliott (Elliott 1997); (E) *V. pinus* type 1 song, Ohio, USA, May, Donald J. Borrer (Borrer & Gunn 1985); (F) *V. pinus* type 2 song, New York, USA, May, Lang Elliott (Elliott 1997); (G) *Leiothlypis celata*, Saskatchewan, Canada, June, John Neville (Neville 2005); (H) *L. crissalis*, Texas, USA, May, William W. H. Gunn (Borrer & Gunn 1985); (I) *L. ruficapilla ruficapilla*, New York, USA, June, Lang Elliott (Elliott 1997); (J) *L. ruficapilla ridgwayi*, Washington, USA, May, Ken J. Hall and Peter R. B. Ward (Hall & Ward 1983); (K) *L. luciae*, Arizona, USA, June, Donald J. Borrer (Borrer & Gunn 1985); (L) *L. virginiae*, Colorado, USA, June, Donald J. Borrer (Borrer & Gunn 1985); (M) *L. peregrina*, Quebec, Canada, June, Lang Elliott (Elliott 1997); (N) *Oreothlypis superciliosa sodalis*, Sinaloa, Mexico, July, John W. Hardy (Hardy *et al.* 1994); (O) *O. superciliosa mexicana*, San Luis Potosí, Mexico, May, Ben B. Coffey (Hardy *et al.* 1994); (P) *O. gutturalis*, Cartago, Costa Rica, March, Kevin J. Zimmer (Hardy *et al.* 1994). X axis in seconds, Y axis in kHz.

and the plain species forming the northern/western clade should be placed in separate genera, and that *P. gutturalis* and *P. superciliosa* form a third group. The 'plain' species and *P. gutturalis* and *P. superciliosa* are sister groups and thus may be combined in a single genus or, alternatively, be recognised as two genera.

All three groups strongly differ in plumage (e.g. Curson *et al.* 1994). *V. pinus* and *V. chrysoptera* have distinctive head and wing patterns that are not found in any of the species of the two other groups. The six 'plain' species lack distinctive features, although some have a yellow (*V. crissalis*) or rufous (*V. luciae*) rump, or a (concealed) rufous crown patch (*V. celata*, *V. ruficapilla*, *V. crissalis*, *V. luciae*). *P. gutturalis* and *P. superciliosa* are colourful species. Adult male *P. gutturalis* has a black mantle and lores, and a bright orange throat and upper breast. Adult male *P. superciliosa* has an olive-green mantle, a broad white supercilium, a bright yellow throat and breast, with a distinctive chestnut mark across the breast.

The three groups can also be distinguished by their songs. *V. pinus* and *V. chrysoptera* have two types of song (Gill & Lanyon 1964). Type 1 songs (Fig. 1c and 1e) seem to be used primarily in the early breeding season in male–female communication (Ficken & Ficken 1969, Gill & Murray 1972a). Type 1 songs are characterised by two (*V. pinus*) or more (*V. chrysoptera*) buzzes of short duration (<0.5 seconds) over a narrow-frequency band (<2 kHz). Type 2 songs (Fig. 1d and f) are more prevalent after incubation and function primarily in male–male interactions (Ficken & Ficken 1969, Gill & Murray 1972a). Type 2 songs of both species also include buzzes. The characteristics of the buzzes of type 1 and 2 songs were described in detail by Gill & Murray (1972b).

Songs of *P. gutturalis* and *P. superciliosa* consist of a single buzzy trill (Fig. 1n–p), which differs from the buzzes of *V. pinus* and *V. chrysoptera* in having a broad-frequency band (>3 kHz) and a longer duration. The total duration of the songs of *P. gutturalis* and *P. superciliosa*, however, is shorter than that of *V. pinus* and *V. chrysoptera*.

Songs of the six 'plain' species of the northern/western clade differ strongly from those of the other two clades by their lack rapid buzzes and their much slower tempo (Fig. 1g–m). As a result, songs of the 'plain' species are much clearer and separate notes can be discerned by human listeners. In addition, song notes of the 'plain' species are more com-

plex than those of the other two clades, and often have both upslurred and downslurred elements. Furthermore, the duration of songs of the 'plain' species is more than 50% longer than that of *P. gutturalis* and *P. superciliosa*. The average song duration of all species in the 'plain' clade is 1.5 seconds or more (Stein 1968; pers. obs.), whereas 25 songs of *P. gutturalis* and 61 songs of *P. superciliosa* measured by the author were all less than 1.0 second (*P. gutturalis*, average 0.9 seconds, $n=3$; *P. superciliosa*, average 0.6 seconds, $n=7$). In fact, the songs of the 'plain' species are as distinct from those of *P. gutturalis*/*P. superciliosa* as they are from *V. pinus*/*V. chrysoptera*.

Thus, the three groups defined by molecular phylogeny are supported by differences in morphological and multiple acoustic characteristics. The dichotomy between the six 'plain' species and *P. gutturalis*/*P. superciliosa* is further underscored by a difference in migratory behaviour: all six 'plain' species are migrants, whereas both *P. gutturalis* and *P. superciliosa* are resident. On these grounds, I contend that the six 'plain' species and *P. gutturalis* and *P. superciliosa* should not be included in a single genus, and that all three groups be recognised as separate genera.

The position of Bachman's Warbler *V. bachmanii* has not been analysed using phylogenetic methods. However, from its plumage pattern, especially the presence of black on the throat and upper breast of the male, and its song, which consists of a series of short, narrow-frequency band buzzes (Fig. 1a–b) reminiscent of *V. chrysoptera* (Fig. 1c) and *V. pinus* (Fig. 1e), *V. bachmanii* is probably more closely related to *V. chrysoptera* and *V. pinus* than to the other two clades.

Nomenclatural consequences

The type species of *Vermivora* Swainson is *Certhia pinus* Linnaeus, 1766 (currently *Vermivora pinus*; see Oberholser 1905). Consequently, the generic name *Vermivora* should be restricted to *V. pinus* and *V. chrysoptera* and, provisionally, *V. bachmanii*. The names *Helminthophaga* Cabanis, 1851 (type: *Motacilla chrysoptera* Linnaeus, 1766, currently *Vermivora chrysoptera*) and *Helminthophila* Ridgway, 1882 (replacement name for *Helminthophaga* Cabanis, preoccupied) are synonyms of *Vermivora* (Oberholser 1905, Hellmayr 1935).

The name *Oreothlypis* Ridgway, 1884 (type species *Compothlypis gutturalis* Cabanis, 1860), which currently rests in the synonymy of *Parula* or *Vermivora* (depending on the generic placement of *P. gutturalis*), is available for *P. gutturalis* (Cabanis, 1860) and *P. superciliosa* (Hartlaub, 1844). The name *Oreothlypis* should be reinstated for *O. gutturalis* and *O. superciliosa*.

No generic name has been proposed for the clade formed by the six 'plain' species (Ridgway 1902, Hellmayr 1935, Lowery & Monroe 1968). Therefore, I propose a new genus taxon for this clade.

Leiothlypis, gen. nov.

Type species

Sylvia peregrina Wilson, 1811 (currently *Vermivora peregrina*).

Diagnosis.—Differs from *Oreothlypis* (*O. gutturalis* and *O. superciliosa*) in plain plumage without black markings on the head, upperparts and underparts. Differs from *Vermivora* (*V. pinus*, *V. chrysoptera*, *V. bachmanii*) in the plain head and wing pattern.

Taxonomic content.—The genus *Leiothlypis* includes six currently recognised species: *L. peregrina* (A. Wilson, 1811), *L. celata* (Say, 1823), *L. ruficapilla* (A. Wilson, 1811), *L. virginiae* (S. F. Baird, 1860), *L. crissalis* (Salvin and Godman, 1889) and *L. luciae* (J. G. Cooper, 1861).

Etymology.—The name *Leiothlypis* is derived from the Greek *λεῖος*, meaning plain and the Greek *θλυπίς*, the name of a kind of finch said to be found in the codices of Aristoteles (Stejneger 1884). The gender of the name *Leiothlypis* is feminine.

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Address: Stevenshof 17, 2312 GM Leiden, The Netherlands, g.sangster@planet.nl